



Biodiversity responds to increasing climatic extremes in a biome-specific manner

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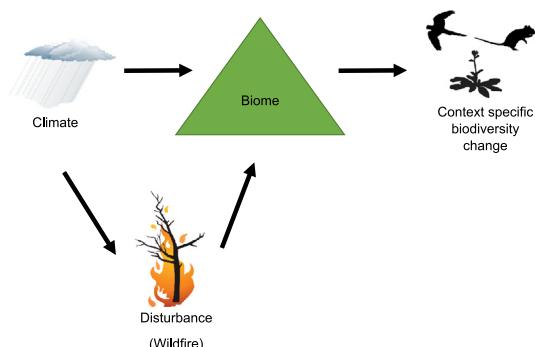
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HIGHLIGHTS

- An increase in the frequency of extreme weather events in all biomes studied.
- Biodiversity changes driven by climate, wildfire or both, varied among biomes.
- Biodiversity responded to recent climate change either directly or indirectly.
- There was no evidence of non-linear change in biodiversity to disturbance.
- Long-term data are essential for detecting biotic responses to environmental change.

GRAPHICAL ABSTRACT



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ABSTRACT

An unprecedented rate of global environmental change is predicted for the next century. The response to this change by ecosystems around the world is highly uncertain. To address this uncertainty, it is critical to understand the potential drivers and mechanisms of change in order to develop more reliable predictions. Australia's Long Term Ecological Research Network (LTERN) has brought together some of the longest running (10–60 years) continuous environmental monitoring programs in the southern hemisphere. Here, we compare climatic variables recorded at five LTERN plot network sites during their period of operation and place them into the context of long-term climatic trends. Then, using our unique Australian long-term datasets (total 117 survey years across four biomes), we synthesize results from a series of case studies to test two hypotheses: 1) extreme weather events for each plot network have increased over the last decade, and; 2) trends in biodiversity

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will be associated with recent climate change, either directly or indirectly through climate-mediated disturbance (wildfire) responses. We examined the biodiversity responses to environmental change for evidence of non-linear behavior. In line with hypothesis 1), an increase in extreme climate events occurred within the last decade for each plot network. For hypothesis 2), climate, wildfire, or both were correlated with biodiversity responses at each plot network, but there was no evidence of non-linear change. However, the influence of climate or fire was context-specific. Biodiversity responded to recent climate change either directly or indirectly as a consequence of changes in fire regimes or climate-mediated fire responses. A national long-term monitoring framework allowed us to find contrasting species abundance or community responses to climate and disturbance across four of the major biomes of Australia, highlighting the need to establish and resource long-term monitoring programs across representative ecosystem types, which are likely to show context-specific responses.

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1. Introduction

Environmental changes during the 21st century are projected to be comparable in magnitude to those of the largest recorded global change that occurred 65 million years ago, and to increase at rates 10–100 fold faster (Diffenbaugh and Field, 2013). The unprecedented rate of global environmental change predicted for the next century is coupled with increases in the unpredictability of climatic events and increases in extreme weather (Urban, 2015). Ecosystem responses to these changes are highly uncertain and challenging to predict (Walther et al., 2002). A range of linear and non-linear ecosystem responses to environmental change potentially exist (Scheffer and Carpenter, 2003). Non-linear responses are characterised by large changes in ecosystem properties in response to a small range of environmental change, in contrast to relative insensitivity outside that critical range of environmental conditions. This threshold behavior is sometimes linked to hysteresis, allowing alternative stable states to persist under the same environmental conditions. 'Regime shifts' between such states may be triggered either by gradual environmental change until a threshold is reached, or by disturbance events (Scheffer and Carpenter, 2003). Ecosystems that display these kinds of responses are challenging to manage because points of change are difficult to predict and reversal of state changes could necessitate major manipulations that may not be feasible (Suding and Hobbs, 2009).

Long time-series of ecological data offer an opportunity to investigate drivers of change and to provide a meaningful context for interpreting trends. Time series data are also appropriate to explore beyond considerations of central tendencies (Pearson and Dawson, 2003) and are paramount for understanding how the extreme highs and lows of temperature or precipitation may drive biodiversity responses (Greenville et al., 2013; Wardle et al., 2013). Such understanding of ecosystem drivers and mechanisms of change is critical for developing more-reliable predictions about ecosystem structure and function in future (Keith et al., 2008, 2013). This, in turn, will better inform decisions on climate adaptation which, to be effective, must be cognisant of the likelihood of synergistic effects among existing processes and legacies from past events (Sala et al., 2012; Monger et al., 2015). It is therefore essential that investment in environmental monitoring programs be sophisticated enough to improve mechanistic knowledge, not simply detect change.

The world's climate has changed. Global mean temperatures have increased by 0.85 °C from 1880 to 2012 due to anthropogenic activities (IPCC, 2014), and these increases, combined with changes in global rainfall patterns, have changed disturbance regimes (Bowman et al., 2014). There has also been an increase in the frequency and magnitude of extreme climate events such as floods and heat waves (IPCC, 2014; CSIRO and Bureau of Meteorology, 2015). Understanding the effects of changes in climate and disturbance regimes on biota can only be provided by long time-series of ecological observations or experiments (Lindenmayer and Likens, 2010; Lindenmayer et al., 2012). Such insight will be vital for identifying species and ecosystems at risk of collapse and for informing mitigation measures.

Here, we use case studies drawn from the Australian Long Term Ecological Research Network (ILTERN) to examine ecosystem responses to changes in climate and disturbance regimes. We first compare climatic variables recorded annually at each plot network during its period of operation, and place these in the context of long-term climatic trends. Then, we raise and test the following hypotheses:

1. The number of extreme weather events recorded by each plot network has increased over the last decade;
2. Trends in biodiversity will be associated with recent climate change, either directly or indirectly through climate-mediated disturbance (e.g., wildfire) responses. We examined biodiversity responses to environmental change for evidence of non-linear behavior.

Using insights gained from long-term datasets, we consider management implications for long-term monitoring in conservation organisations that seek to maintain species populations that are likely to face increases in extreme weather events and an increasingly unpredictable climate.

2. Methods

Long-term data (10–35 years) were obtained from five of the 12 Australian LTERN plot networks (Lindenmayer et al., 2014). These five plot networks monitor biodiversity in tropical savannas and heathlands, deserts, alpine systems, temperate heathlands and temperate woodlands, representing half of the major Australian biomes defined by Olson et al. (2001) (Fig. 1).

2.1. Climate

To compare the climate at each plot network during their survey years in relation to longer-term climate trends, annual climate data from 1970 to 2014 were extracted for each of the five plot networks using ANUCLIM 6.1 (Xu and Hutchinson, 2013). ANUCLIM data were used instead of data from the nearest Bureau of Meteorology weather station (distance to plot range 5–217 km), as it provided a standardised dataset with equal length for each plot network. For each plot network, we constructed density histograms for a suite of climate variables (annual rainfall, mean annual temperature, mean minimum temperature, and mean maximum temperature). For the Alpine Plot Network, snow depth data from the Falls Creek (1954–2011; http://gergs.net/wp-content/uploads/2014/04/Rocky_Valley_peak_trend.png) and Mt. Hotham (2012–2016; <http://www.mthotham.com.au/all-about-hotham/snow-weather/snow-charts/>) weather stations were combined to make a complete time-series from 1954 to 2016, and this was used instead of rainfall at that site. Depth of snow cover determines over-wintering habitat suitability for alpine biota such as small mammals (Shi et al., 2015), so we used this instead of rainfall as a key measure of environmental change. These two snow weather stations were chosen because they are close to each other (~10 km) and their annual precipitation records are highly correlated ($r = 0.92$).

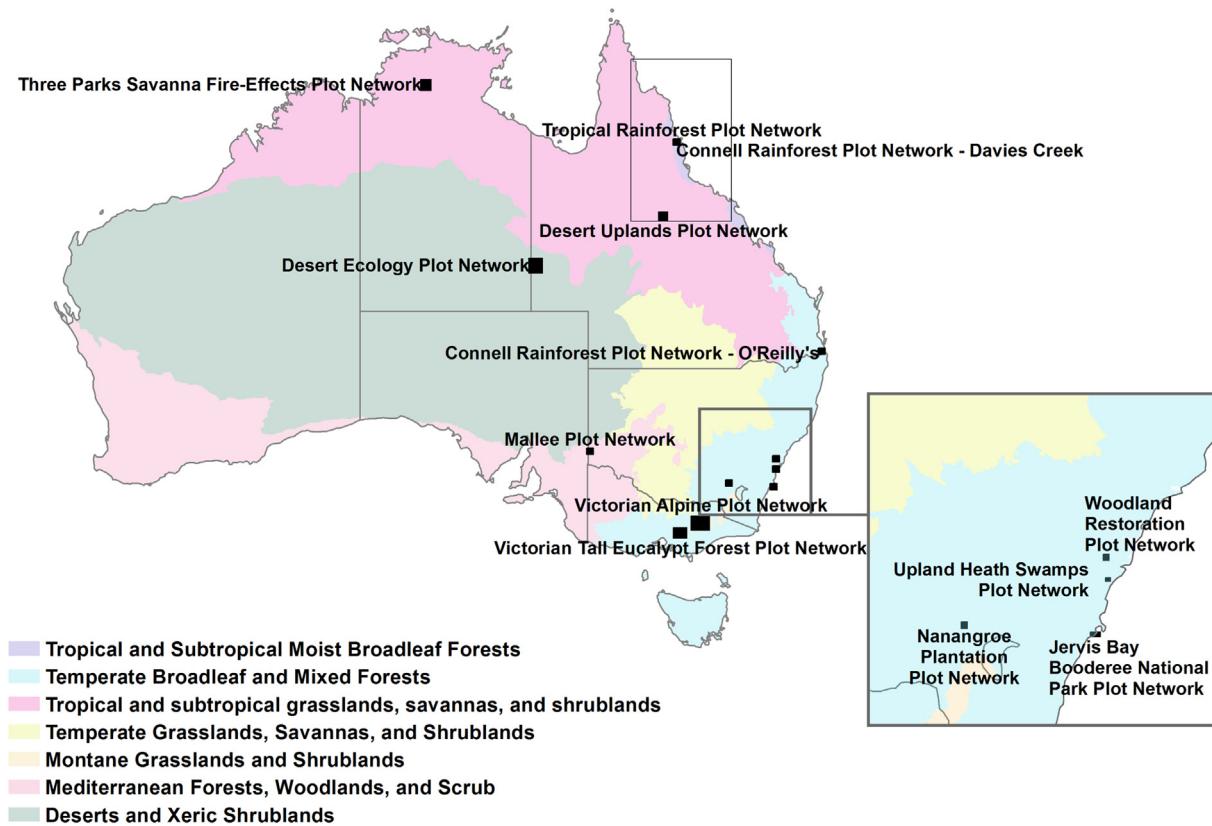


Fig. 1. Location of each Australian LTERN Plot Network (black filled boxes and rectangle) superimposed over a map of the continent's biome distributions (from Olson et al., 2001).

The time-series of ANUCLIM data for each plot network site were divided into two periods: surveys prior to 2005 (10–25 years) and surveys conducted from 2005 to 2016 (10 years). Together, these encompass the entire period over which ecological observations were recorded. These periods were chosen because there has been a significant increase in global decadal temperatures across the last three decades, especially over the last decade (IPCC, 2014). Lastly, we calculated the percentage of years during which surveys were carried out at each plot network when extreme climate events (long-term 10th or 90th percentile, see Greenville et al. (2012)) were experienced within each rainfall (snow) and temperature category.

2.2. Biodiversity

Ecosystem-specific methods were employed at each of the five plot networks to maximize their sensitivity to detect and diagnose ecological change (see Lindenmayer et al., 2014). The individual plot networks were originally set up to study different taxa and were brought together in 2012 under LTERN. Hence different species and approaches were used for each plot network. It was deemed important to continue using the original methods and approaches to retain the integrity of the temporal datasets for each long-term plot network, rather than disrupt the temporal dataset by imposing a common monitoring protocol. Thus, the biodiversity datasets for each plot network were analysed separately. If available, climate datasets were obtained from on-site weather stations or the closest Bureau of Meteorology weather station to the study region. This was necessary because the modelled ANUCLIM data do not capture the small-scale climate variation for individual survey locations for some plot networks.

2.2.1. Three Parks Savanna Fire-Effects Plot Network

The Three Parks Savanna Fire-Effects Plot Network focuses on assessing the relationships between fire regimes and characteristics of

tropical savanna vegetation and the vertebrate fauna in three north Australian conservation reserves—Kakadu, Litchfield and Nitmiluk National Parks (Russell-Smith et al., 2014). Fauna data included sampling at 151 plots (24 plots at Nitmiluk National Park, 27 Litchfield National Park, 100 Kakadu National Park); and flora data included sampling from 34 of the 151 plots within sandstone heath vegetation on the Arnhem Plateau (Kakadu National Park, Fig. 1).

The flora surveys were performed at long-term monitoring plots (40 × 10 m) which were established in 1994–95 and re-sampled at 5-year intervals, over a 20-year period, following methods described in Russell-Smith et al. (2014). Only data for fire interval-sensitive species of obligate seeder taxa requiring at least three years to attain sexual maturity after germination are considered here. Generally, wildfires occurring at frequencies shorter than the required maturation periods of obligate seeder taxa result in significant impacts on population sizes and site persistence of species (Russell-Smith et al., 2012; Keith et al., 2014). Importantly, the annual monsoon rainfall season is highly predictable in the study region, delivering at least 1000 mm in any one season over a 5–6 month period.

Vertebrate surveys were performed at plots (50 × 50 m) installed adjacent to the flora monitoring plots, and were also re-visited at 5-year intervals using procedures described by Woinarski et al. (2010). The trapping period ranged from 48 to 72 h among plots but was consistent at each plot between survey sessions. For 72-h surveys, 20 Elliott traps (33 cm × 10 cm × 9 cm) were placed equidistantly around the perimeter of the plot, and a cage trap (56 cm × 20 cm × 20 cm) placed at each corner, and two 20 L pitfall traps (30 cm wide and 36 cm deep, with 8 m of drift-line fence) placed within the plot. For 48-h surveys, the same number of trap nights was achieved with 30 Elliott traps, 6 cage traps and 3 pitfall traps. Cage and Elliott traps were baited with a mixture of peanut butter, honey and oats, and all traps checked within 1 h of dawn on each sampling day. All captured mammals were identified and released at the point of capture, without being marked. In

addition to trapping, two 10 min spotlight searches were performed (Woinarski et al., 2010).

Data for 25 small mammal species (mass < 5 kg, see Woinarski et al. (2010)) are considered here. Change in small mammal abundance (all species combined) and species richness was calculated as the difference between the value at the first (2001–2004) and last (2012–2014) survey, with an intervening period of 10–11 years at each plot, following the methods in Russell-Smith et al. (2014). Of 151 plots across the three National Parks, 30 plots (12 Nitmiluk National Park and 18 Kakadu National Park) were excluded from small mammal analysis as change could not be calculated due to values of zero species richness or abundance at both the start and end of the monitoring period.

To calculate change in the numbers of obligate seeder plant taxa, the difference between the value at the first (t_1) and last measurement (t_5) was calculated for each plot, as described in Russell-Smith et al. (2012). Observations of fire incidence at plots were made annually (Russell-Smith et al., 2012, 2014). For flora, fire frequency was defined as the number of times that each plot was burnt over the 20-year period. For fauna, fire frequency was defined as the proportion of times each plot had been burnt in the intervening period, because plot sampling was staggered over several years and not all plots were sampled each round. The proportion of times each plot had been burnt in the intervening period was derived by mapping of burn scars from MODIS Satellite imagery in ArcGIS.

To test the relationship between fire frequency and numbers of obligate seeder plant taxa, small mammal abundance and small mammal species richness, linear regression was performed in R version 3.3.2 (R Core Team, 2017). Inspection of diagnostic plots indicated no evidence of non-linear relationships and normally distributed response variables, so a Gaussian error structure was applied. To control for differences in initial small mammal captures between plots, we included the starting value of the response in each fauna model (i.e., the first capture abundance or species richness recoded at a plot). Inspection of diagnostic plots indicated that all models met statistical assumptions of normality and homoscedasticity (Zuur, 2009).

2.2.2. Desert Ecology Plot Network

The Desert Ecology Plot Network aims to quantify changes in climate, population dynamics and species interactions in resource-pulse environments to inform conservation management within rangelands. Live-trapping was carried out at 11 sites across Carlo Station, Tobermorey Station, Cravens Peak and Ethabuka Reserves, and covered an 8000 km² area of the northeastern Simpson Desert in southwestern Queensland (Fig. 1). Small mammals were live-trapped using pitfall traps (16 cm diameter, 60 cm deep), each equipped with a 5 m drift fence of aluminum flywire to increase trap efficiency (Friend et al., 1989).

Each trap was opened for 2–6 nights per sampling occasion. To account for unequal trapping effort, live-capture counts were standardised per 100 trap nights (TN: trap nights = traps \times nights opened) to yield a capture rate, and averaged for each year. The original motivation for the sampling regime, the characteristics of the sites, sampling methods and key results are described in detail elsewhere, with summaries in Dickman et al. (2014) and Greenville et al. (2016). We limit our datasets here to the two most common species of rodent, *Pseudomys hermannsburgensis* (sandy inland mouse, Family: Muridae) and *Notomys alexis* (spinifex hopping-mouse, Family: Muridae), as their numerical dominance and rapid response to rainfall provide suitable characteristics to detect long term population change.

Daily data from automatic weather stations (Envirodata, Warwick, Queensland) at each site were used to calculate total annual (calendar year) rainfall antecedent to capture. Weather stations were active from 1995 to 2016. To obtain rainfall data before 1995 for Main Camp, where trapping started in 1990, we averaged daily rainfall records from the closest weather stations at Glenormiston, Sandringham, Boulia, Bedourie, and Birdsville (Bureau of Meteorology, 2016). The 1-

yr lag was used to account for the time required for small mammals to respond, via breeding, to a large rainfall event, and has been used successfully to predict mammal captures in previous studies (Greenville et al., 2012, 2016).

Piecewise regression was used to identify thresholds in annual rainfall at which rodents showed numerical responses (i.e., changes in capture rate), as described in Greenville et al. (2012). A threshold relationship was predicted as extreme rains and temperatures (>90th quantile) are more likely to drive small mammal populations in arid Australia than are moderate rains; consequently, simple linear relationships probably do not occur (Greenville et al., 2012). Piecewise regressions use two or more lines, joined at a break point, that can be used to identify thresholds (Toms and Lesperance, 2003). We used piecewise regressions with one knot, or break point, that could occur at any value of rainfall. The break point was estimated from likelihood-ratio statistics (Toms and Lesperance, 2003). Confidence intervals were estimated from 1000 bootstrap samples. Piecewise regressions were performed using SiZer 0.1–4 (Sonderegger, 2011) in R version 3.3.2 (R Core Team, 2017).

2.2.3. Alpine Plot Network

One of the aims of the Alpine Plot Network is to determine long-term patterns in the population ecology of *Burramys parvus* (mountain pygmy-possum, Family: Burramyidae) at Mt. Hotham, Victoria, to ensure effective conservation management of this critically endangered species. In addition to *B. parvus*, other small mammals are captured as part of the monitoring program and we also present data for *Rattus fuscipes* (bush rat, Family: Muridae), which was captured in sufficient numbers for comparison.

Burramys parvus is the only Australian mammal species confined to alpine environments. Thought to be extinct, it was rediscovered in the early 1960s near Mount Hotham (Heinze et al., 2004). The species occurs in periglacial boulder fields (basalt, granite, granodiorites) overlain with mountain plum-pine (*Podocarpus lawrencei*) heathland and adjacent alpine communities, such as boulder fields, that provide a favourable microclimate (Shi et al., 2015). Its diet in spring-summer predominantly comprises Bogong moths (*Agrotis infusa*), with other invertebrates, seeds and fruits being important in late summer and autumn. Females normally have one litter of four young following snowmelt in spring. All individuals accumulate subcutaneous fat during late summer and autumn, and spend the winter in hibernation (about 7 months for adults and 5 months for juveniles (Geiser and Broome, 1991). Snow cover provides important insulation and protection to hibernating animals (Shi et al., 2015).

In contrast to *B. parvus*, *R. fuscipes* is a widespread and common species of coastal and montane forest, heathland, rainforest and alpine areas of Australia (Strahan, 2004). In alpine and sub-alpine habitats, the bush rat is a generalist fungivore, but it can also consume invertebrates, grasses and seeds (Carron et al., 1990). *Rattus fuscipes* can breed throughout the year, but most breeding in alpine regions is in the Austral spring-autumn (Happold, 2011, 2015).

Systematic surveys for *B. parvus* and *R. fuscipes* commenced in Victoria in 1982 at Mt. Hotham (Fig. 1). Initially, trapping frequency was monthly during the snow-free period, but since about 1987, surveys generally coincided with the breeding season of *B. parvus* (Nov-Dec). The standard trapping grid (0.25 ha), as described by Mansergh (1989). This consists of three 100 m lines from 1982 to 1982, six lines from 1984 to 1985, seven lines from 1986 and eight lines from 1987 onwards. Each 12.5 m apart, with Elliott traps placed at 5 m spacing (= 60 traps). Typically, trapping occurs for three to five days (= 180–800 trap-nights per visit). The sex, breeding status, identity and weight are recorded for each individual animal.

Captures of *B. parvus* and *R. fuscipes* were standardised for differences in survey effort (captures per 100 trap nights, see Section 2.2.2) over the study period. To investigate the relationship between captures and maximum snow depth, maximum annual temperature and survey

year, generalized linear models were used with a Gaussian distribution. No evidence of collinearity was found between maximum snow depth and mean maximum temperature ($r < 0.7$). Snow depth data from the Falls Creek (1982–2011) and Mt. Hotham (2012–2016) weather stations were combined and temperature data was obtained from ANUCLIM 6.1 (Xu and Hutchinson, 2013), as described in 2.1. Analyses were performed in R version 3.3.2 (R Core Team, 2017). Inspection of diagnostic plots indicated that all models met statistical assumptions of normality and homoscedasticity (Zuur, 2009).

2.2.4. Upland Heath Swamps Plot Network

The Upland Heath Swamps Network aims to understand the effects of alternative fire regimes and how plant responses can be characterised by trends in functional groups of species. The study was conducted in an area of fire-prone coastal wet heathland (c. 70 m above sea level) in Royal National Park, New South Wales, Australia (Fig. 1). The vegetation in the area is fire-prone and characterised by sclerophyllous shrubs and graminoids, with the herbaceous understorey dominated by species of Restionaceae, Cyperaceae and Poaceae. Large shrubs of *Banksia*, *Hakea*, *Allocasuarina* and *Leptospermum* begin to form dense canopies within 5–6 years post fire (Keith and Bradstock, 1994; Keith et al., 2007). The herbaceous component, the subject of this analysis, was divided into three plant functional types (based on Keith et al., 2007): fire ephemerals (PFT 4), perennial resprouting herbs (PFT 6) and rhizomatous resprouters (PFT 5). We focused on herbaceous plant species because these are much neglected components of heathland biota, relative to the dominant sclerophyll shrubs which have been extensively studied at the population level (e.g. Keith et al., 2014). The herbaceous flora was expected to be sensitive to fire regimes, directly and indirectly. The direct mechanisms involve the effects of fire on contrasting life-history traits among the three functional groups, particularly seed dormancy, mechanisms of vegetation recovery and spread, and longevity of standing plants (Keith et al., 2007). The indirect mechanisms involve competitive effects from the dominant sclerophyll shrubs, which overtop and reduce light to the herbaceous layer (Keith et al., 2007). The soils, which derive from sandstone, tend to be highly infertile, siliceous and seasonally wet over the winter months. Soil water deficit over summer varies markedly among years, depending on rainfall inputs connected with El Niño cycles and other sources of variation. The topography is relatively flat and hence surface runoff is slow, creating waterlogged conditions during periods of sustained rainfall.

In 1990, 56 permanent 0.25 m² plots were established along eight transects within a 4 ha area of heathland. Since 1990, the total abundance (number of clustered individuals, single- or multi-stemmed) of all herbaceous species within each plot has been censused on 13 separate occasions (1990–2016) (Keith and Tozer, 2012). Wildfires in October 1988 (prior to the first census) and January 1994 burnt the entire site (all 56 plots), with subsequent planned fires in April 2006 (25 plots) and September 2015 (24 plots) burning parts of the site. The 1994 fire occurred prior to the census of that year.

Time since fire was calculated by assessing when (year) each plot was burnt in a wildfire or hazard reduction burn. Annual rainfall data were compiled from the closest weather station at Audley, Royal National Park (Bureau of Meteorology, 2016) and rainfall from the prior year was used to account for the time required for vegetation to respond, via growth, to a rainfall event. All variables were standardised by subtracting the mean and dividing by the standard deviation (z-scores) to allow direct comparisons between factors and to allow model convergence. Generalized linear mixed models (GLMMs) were used to determine if the numbers of clumps of each plant functional type (PFT) were influenced by “annual rainfall from prior year”, taking into account “time (years) since fire”. Site (transect) was entered as a random factor to account for plot-level variation, such as those related to fire intensities or timing. Analysis was performed using the package lme4 version 1.1–18 (Bates et al., 2015) in R version 3.3.2 (R Core Team, 2017). Inspection of diagnostic plots indicated that all models

met statistical assumptions of normality and homoscedasticity (Zuur, 2009).

2.2.5. Nanangroe Plantation Plot Network

The Nanangroe Plantation Plot Network aims to quantify the inter-relationships between human disturbance, landscape-based management intervention, and changes in vegetation condition and biodiversity response in temperate woodlands. The Nanangroe region lies 10–20 km southeast of the town of Jugiong in southern New South Wales, southeastern Australia (Fig. 1). The area is characterised by a temperate climate (hot summers and relatively cool winters). Prior to disturbance, the original vegetation cover included temperate woodland vegetation types, dominated by *Eucalyptus* species. Further details of the study area can be found in Lindenmayer et al. (2008).

In 1998, prior to commencement of landscape transformation to a pine-dominated system by the then-State Forests of New South Wales, 55 of the 70 remnant woodland patches were selected randomly, and stratified by vegetation class and woodland patch size. These 55 patches were exempt from clearing while plantation establishment was undertaken in the surrounding areas. The patches varied in dominant vegetation type, including yellow box (*Eucalyptus melliodora*), red box (*E. polyanthemos*), white box (*E. albens*), Blakely's red gum (*E. blakelyi*), apple box (*E. bridgesiana*) and long-leaf box (*E. goniocalyx*). In addition, there were patches dominated by red stringybark (*E. macrorhyncha*), broad-leaved peppermint (*E. dives*), and river oak (*Allocasuarina cunninghamiana*).

Birds are the biodiversity component assessed here. To survey birds, a permanent 200 m transect was established within each woodland patch. For each survey, two observers each visited three points at 0 m, 100 m and 200 m along the transect on different days, typically 2–4 days apart. At each point, the observer recorded all species detected in a 5 min interval and within 50 m of the point. Field surveys were completed in early November every two years from 1999 until 2013. Early November is the peak breeding season in the study region, when summer migrants are present, and birds have established territories and exhibit strong patterns of site fidelity (Lindenmayer et al., 2008). Detections were made between 05.30 and 09.30 h and were not undertaken on days of poor weather (rain, high wind, fog or heavy cloud cover). The order in which particular sites were surveyed on any particular day was randomized.

Highly experienced observers completed surveys of forest and woodland birds. These observers differed in their ability to detect some groups of birds, but Lindenmayer et al. (2009) showed that pooling counts of two or more observers at the same plot point could compensate for variability due to observer heterogeneity.

Crested pigeon (*Ocyphaps lophotes*), black-faced cuckoo-shrike (*Coracina novaehollandiae*), noisy friarbird (*Philemon corniculatus*), rufous whistler (*Pachycephala rufiventris*) and white-plumed honeyeater (*Lichenostomus penicillatus*) were expected to be sensitive to climate variation in part because of their dependence on the availability of food resources such as nectar, pollen and invertebrates that can be strongly influenced by climatic conditions. For each of these five species, the reporting rate was calculated as the proportion of sites (expressed as a %) where there was positive evidence (observed at least once) of the species; we then computed the reporting rate for each survey following the method of Lindenmayer and Cunningham (2011). As for climate (Section 2.1), annual rainfall, and annual mean, maximum and minimum temperatures from the study region were obtained from ANUCLIM 6.1 (Xu and Hutchinson, 2013).

Species reporting rate, climate (annual rainfall and mean temperature) and survey year were modelled as proportional odds and a quasi-binomial GLMM was used, as the data were over-dispersed (Zuur, 2009). Annual rainfall and annual maximum temperature, annual temperature and annual maximum temperature, annual temperature and annual minimum temperature showed high levels of collinearity ($r > 0.7$), and thus only annual rainfall and temperature

were used in the final analysis. To aid in assessing trends in bird species reporting rates, a loess smoother was plotted for species reporting rate per year. Analysis was performed using the package *lme4* version 1.1–18

([Bates et al., 2015](#)) in R version 3.3.2 ([R Core Team, 2017](#)). Inspection of diagnostic plots indicated that all models met statistical assumptions of normality and homoscedasticity ([Zuur, 2009](#)).

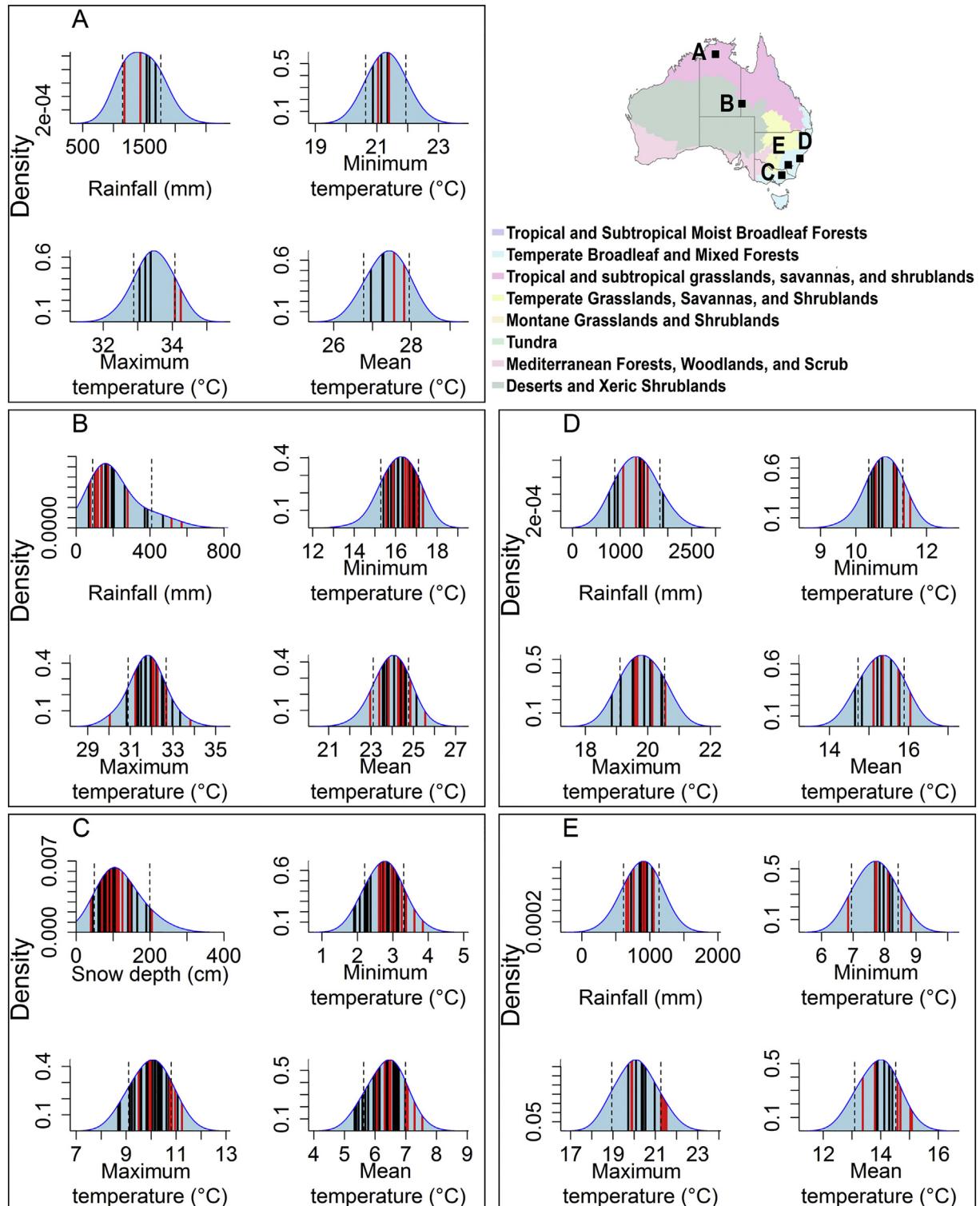


Fig. 2. Each panel shows the density histograms of long-term climate variables for A) Three parks savannah fire-effects, B) Desert ecology, C) Alpine, D) Upland heath swamps and E) Nanangroe plantation Plot Networks. Red lines indicate surveys conducted from 2005 to 2016 and black lines surveys prior to 2005. Dashed vertical lines represent the 10th and 90th percentiles. Climate data were derived from ANUCLIM 6.1, except for snow depth, which was combined from Falls Creek (1954–2011) and Mt. Hotham (2012–2016) weather stations, Victoria, Australia. Insert shows the location of each Australian LTERN Plot Network (black filled boxes with corresponding letters for each Plot Network above), superimposed on a map of biome distributions (from [Olson et al., 2001](#)). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3. Results

3.1. Climate

Across all plot networks, more survey years in the last decade experienced extreme climate events (10th and 90th percentile) than were recorded in the pre-2005 survey years. The increase in extreme climate events within the last decade occurred in all four biomes represented by the five plot networks. Frequency of extreme temperatures increased in all five plot networks, while three networks showed increased frequency of extreme rainfall events. In the Three Parks Savanna Fire-Effects Plot Network, survey years experiencing an extreme climate event increased for mean annual maximum temperatures when comparing pre-2005 surveys (0% of surveys were in extreme years) to post-2005 surveys (100% of surveys were in extreme years). No survey years experienced extreme events for mean annual rainfall, mean annual minimum temperature or mean annual temperature (Fig. 2A).

Comparison of pre-2005 to post-2005 survey years in the Desert Ecology Plot Network showed that the frequency of extreme climate events increased for all variables except minimum temperature (mean annual rainfall: 19% to 27%; mean annual minimum temperature: 13% to 9%; mean annual maximum temperature: 19% to 27%; mean annual temperature: 6% to 36%, respectively; Fig. 2B).

In the Alpine Plot Network, extreme climate events were more frequent in post-2005 years than pre-2005 years for all climate variables (mean annual minimum temperature: 21% to 30%; mean annual maximum temperature: 17% to 40%; mean annual temperature: 17% to 50%; maximum annual snow depth: 17% to 20%, respectively; Fig. 2C).

In the Upland Heath Swamps Plot Network, a higher frequency of extreme events was experienced for temperature variables, but not rainfall, in the post-2005 survey years compared to the pre-2005 survey years (mean annual rainfall: 38% to 0%; mean annual minimum temperature: 13% to 40%; mean annual maximum temperature: 13% to 20%; mean annual temperature: 13% to 20%, respectively; Fig. 2D).

Lastly, survey years in the Nanangroe Plantation Plot Network experiencing an extreme climate event increased for all climate variables (mean annual rainfall: 0% to 0%; mean annual minimum temperature: 0% to 43%; mean annual maximum temperature: 0% to 57%; mean annual temperature: 0% to 57%, respectively; Fig. 2E), except rainfall, for post-2005 survey years compared with pre-2005 survey years.

3.2. Biodiversity

3.2.1. Three Parks Savanna Fire-Effects Plot Network

The number of obligate seeders per plot decreased most at sites that were burnt most frequently over the 20-year study period (GLM: slope = -0.15 , $F = 5.12$, $P = 0.03$; Fig. 3a). Change in small mammal abundance and richness was significantly related to the frequency of fire that occurred in the 10–12 years between repeat sampling (GLM: Δ Abundance slope = -2.91 , $t = -2.76$, $P = 0.01$; Δ Richness slope = -1.02 , $t = 0.36$, $P = 0.01$), with an overall pattern of decreased abundance and richness at sites with more frequent fire (Fig. 3b, c). The initial abundance of small mammals at a plot also had a significant effect on small mammal abundance (GLM: slope = -0.83 , $t = -15.89$, $P < 0.01$) and richness (GLM: slope = -1.01 , $t = -13.75$, $P < 0.01$). Change in abundance was predominantly negative at fire frequencies above 0.25 (i.e., when fire occurred in >25% of years), and change in richness was predominantly negative at fire frequencies above 0.3 (Fig. 3b, c).

3.2.2. Desert Ecology Plot Network

Over the 26-year study period, the two species of rodents irrupted 3–4 times (Fig. 3d, e). Line 2 (line after the breakpoint) in the piecewise regressions had a significantly different slope to line 1 (line before breakpoint), indicating support for a significant breakpoint or threshold response (Table 1; Fig. 3f, g). The two rodent species responded positively to antecedent rainfall after reaching a threshold (breakpoint) of

270 mm. However, the threshold of rainfall differed between the two species, with *P. hermannsburgensis* exhibiting greater variation in response (270 mm, CI: 233–552) compared to *N. alexis*: (316 mm, CI: 242–381).

3.2.3. Alpine Plot Network

Capture rates for *B. parvus* and *R. fuscipes* showed contrasting patterns over the survey period (Fig. 3h, i). Captures of *B. parvus* decreased whereas captures of *R. fuscipes* increased (Table 2). Capture rates were not predicted by maximum annual snow depth nor annual mean maximum temperature (Table 2).

3.2.4. Upland Heath Swamps Plot Network

The abundance of clumps of fire ephemerals (PFT 4) and perennial resprouting herbs (PFT 6) decreased during the 21-year study period, while rhizomatous resprouters (PFT 5) varied in a non-linear manner (Fig. 3j, k, l, respectively). The abundance of clumps in the three plant functional types was significantly influenced by the interaction between time-since-fire and antecedent rainfall (Table 3). In general, the abundance of plant clumps decreased with time since fire, but that response was abated by high antecedent rainfall (Fig. 3m, n, o).

3.2.5. Nanangroe Plantation Plot Network

Climate and survey year had contrasting effects on reporting rates for the five species of bird during the 17 year study period (Table 4). The reporting rate for *O. lophotes* increased over the survey period (Table 4; Fig. 3p), whereas that for *C. novaehollandiae* and *P. corniculatus* showed no relationship with survey year or any climate variable (Table 4; Fig. 3q, r). The reporting rate for *P. rufiventer* was associated positively with annual temperature (Table 4; Fig. 3s), whereas the reporting rate declined for *L. penicillatus* (Table 4; Fig. 3t).

4. Discussion

In general, trends in biodiversity were associated with recent climate change, either directly or indirectly through climate-mediated disturbance (wildfire) responses. However, we found no evidence of non-linear responses, suggesting either that tipping points may not exist in these ecosystems or that they have not yet been reached. Instead, the influence of the drivers was context-specific, with some species responding positively to climate variables or fire, and others responding negatively. For example, the species richness of obligate seeder shrubs in the tropical savanna heathlands decreased with increasing fire frequency, after plots were burnt more than three times within the last 20 years. By contrast, clumps of three plant functional types declined in temperate heathlands with increasing time since wildfire, and may continue to do so unless periodic fires trigger release from competition or replenishment of seedbanks or budbanks. Long-term biotic changes across sites are often variable due to the dominance of different species and trophic groups that are present (Peters et al., 2012). This suggests that, although the climate for each Australian biome changed over the last decade, its influence on species within each biome differed.

There was an increase in extreme climate events within the last decade at each plot network. Increases occurred at all sites for temperature variables, but only at some sites for rainfall. If there is a multi-cyclical pattern of climatic variation over our study period, there may be a bias in detecting extreme climate events in pre-2005 survey years given the longer observational period. Despite this potential bias, we observed an increase in extreme climate events within the last 10 years (post-2005 surveys), suggesting our observations of recent climate change may be conservative. In addition, our results showing recent climate change agree with past climate projections (Hughes, 2003; CSIRO and Australian Bureau of Meteorology, 2007, 2012; IPCC, 2014). Below we draw on the specific results for each plot network to discuss the direct and indirect effects of climate change on biota, and then provide insights for conservation and government organisations faced with the

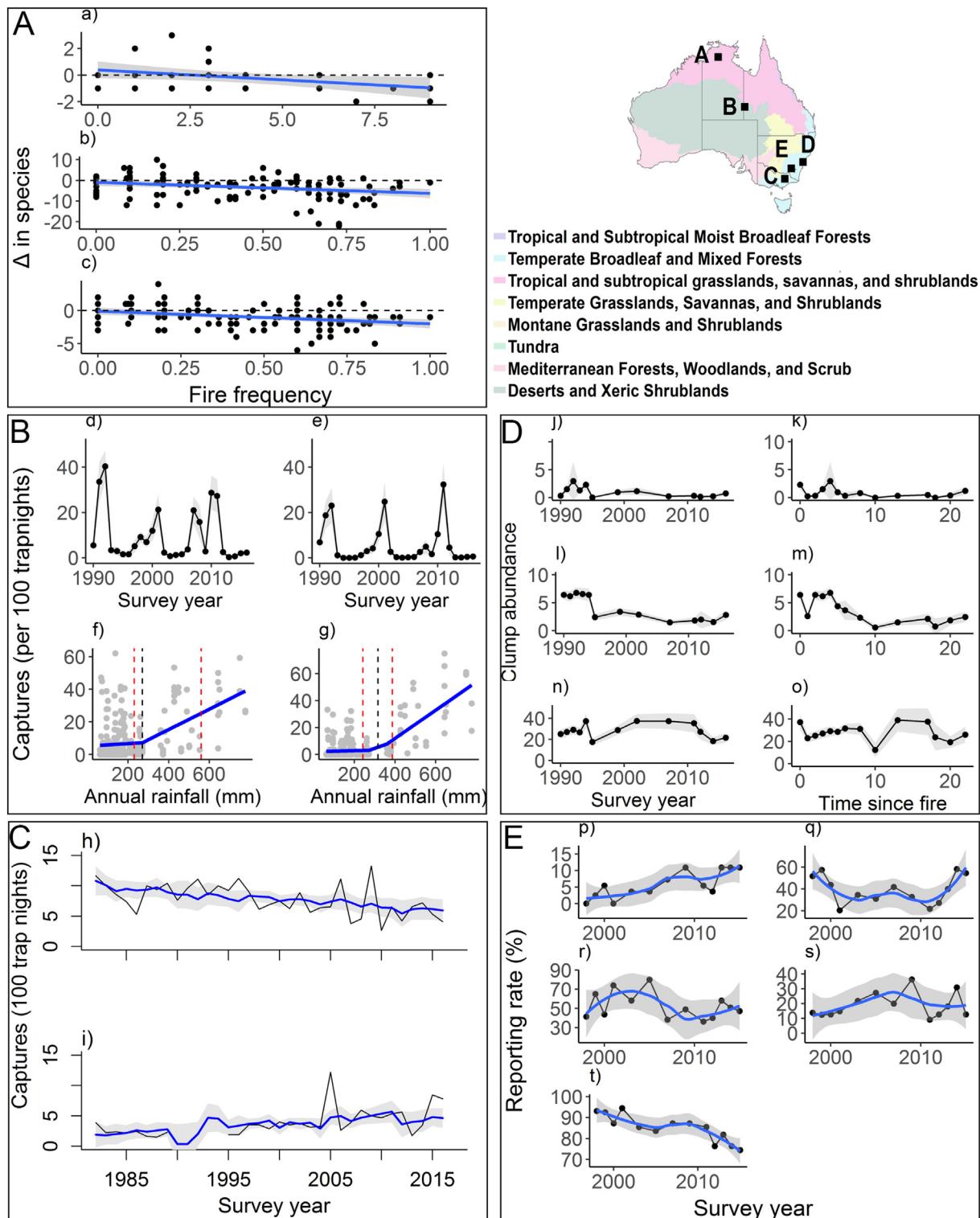


Fig. 3. The role of climate and fire in driving components of biodiversity in five Australian LTERN Plot Network (black filled boxes) case studies. Biomes follow Olson et al. (2001). A) Three Parks Savanna Fire-Effects Plot Network: linear regression results reveal that an increase in fire frequency has led to a decrease in a) numbers of obligate seeders from 1995 to 2014, Kakadu National Park, b) abundance of small mammals and c) small mammal species richness across Nitmiluk National Park, Litchfield National Park and Kakadu National Park, Northern Territory. B) Desert Ecology Plot Network: long-term population dynamics of the rodents d) *Pseudomys hermannsburgensis* and e) *Notomys alexis*, Simpson Desert, Queensland. Piecewise regression revealed that the two rodent species responded to antecedent rainfall after a threshold value was reached for f) *Pseudomys hermannsburgensis* and g) *Notomys alexis*. Dashed black lines indicate threshold values and red dashed lines are 95% confidence intervals. C) Alpine Plot Network: long-term population dynamics of h) *Burramys parvus* and i) *Rattus fuscipes*, Mt. Hotham, Victoria. Captures per 100 trap nights (black line), Generalized Linear model predictions (blue line) and 95% confidence intervals (grey area) are shown. D) Upland Heath Swamps Plot Network: abundance of all herbaceous plant species clumps for fire ephemerals (PFT 4) per j) survey year and k) time since fire, perennial resprouting herbs (PFT 6) for l) survey year and m) time since fire, rhizomatous resprouters (PFT 5) for n) survey year and o) time since fire. E) Nanangroe Plantation Plot Network: Reporting rates for p) *Ocyphaps lophotes*, q) *Coracina novaehollandiae*, r) *Philemon corniculatus*, s) *Pachycephala rufiventris* and t) *Lichenostomus penicillatus*, Gundagai, New South Wales. Blue line represents loess smoother. Grey shaded areas represent 95% confidence intervals for all plots. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1

Desert Ecology Plot Network. Piecewise regression results for *Pseudomys hermannsburgensis* (sandy inland mouse) and *Notomys alexis* (spinifex hopping-mouse) and annual rainfall from the prior year, Simpson Desert, Queensland, Australia. Data are from 11 sites across the 8000 km² study area collected from 1990 to 2016. If $P < 0.05$ for line 1 (line before breakpoint), the slope is significantly different than zero, and if $P < 0.05$ for line 2 (line after breakpoint), the line 2 slope is different from the line 1 slope, and indicates a break point or threshold response. SE = standard error.

Variable	Slope	SE	t	P
<i>Pseudomys hermannsburgensis</i>				
Intercept	5.19	2.01	2.59	0.01
Line 1	0.007	0.01	0.60	0.55
Line 2	0.06	0.02	2.95	0.003
<i>Notomys alexis</i>				
Intercept	2.16	1.34	1.61	0.12
Line 1	0.003	0.008	0.42	0.67
Line 2	0.10	0.10	7.20	<0.01

challenge of managing populations experiencing an increasingly unpredictable climate.

4.1. Direct effect of climate change on biota

Populations of the two species of desert rodent surveyed by the Desert Ecology Plot Network responded to rainfall after reaching a rainfall threshold value. Previous studies have found that captures of Australian desert rodents increase after extreme rainfall events (Greenville et al., 2012, 2013). However, the sandy inland mouse exhibited greater variation in its threshold response than did the spinifex hopping-mouse, suggesting that individual species' life histories are important in mediating precipitation effects.

The frequency of extreme rainfall events increased at the Desert Ecology Plot Network site in post-2005 surveys, and these are projected to increase in the future (IPCC, 2014; CSIRO and Bureau of Meteorology, 2015). Indeed, the magnitude and frequency of extreme rainfall events has increased in central Australia (Greenville et al., 2012), suggesting that the rainfall threshold is, and will be, reached more frequently. However, wildfire risk and populations of introduced predators also increase after extreme rainfall events (Letnic and Dickman, 2006; Greenville et al., 2009; 2014; Letnic et al., 2011), leading to negative feedback loops. Exaggerated population booms and rapid collapses may create conditions that are conducive to stochastic population extinctions at local or regional scales (Xu et al., 2006).

The Alpine Plot Network study showed that the numbers of mountain pygmy-possums (alpine specialists) declined significantly over the survey period at Mt. Hotham (average number of animals captured per 100 trap nights has declined by 30% over 35 yrs), whereas the average number of bush rats (generalists) captured per 100 trap nights almost doubled. The numbers of both species varied with survey year, but not with maximum snow depth or maximum temperature. This

Table 2

Alpine Plot Network: generalized linear model results for captures of *Burramys parvus* (mountain pygmy-possum) and *Rattus fuscipes* (bush rat), and their responses to maximum snow depth, maximum annual temperature and survey year (1982–2016), Mt. Hotham, Victoria, Australia. SE = standard error.

Variable	Slope	SE	t	P
<i>Burramys parvus</i>				
Intercept	265.79	91.44	2.91	0.007
Snow depth	−0.005	0.01	−0.49	0.63
Maximum temperature	0.42	0.72	0.59	0.56
Survey year	−0.13	0.05	−2.76	0.01
<i>Rattus fuscipes</i>				
Intercept	−245.28	88.79	−2.76	0.01
Snow depth	−0.02	0.01	−1.51	0.14
Maximum temperature	−0.83	0.82	−1.01	0.32
Survey year	0.13	0.05	2.75	0.01

Table 3

Upland Heath Swamps Plot Network. Generalized Linear Mixed Model results for the abundance of herbaceous plant species clumps and response to annual rainfall and time since fire (1990–2016), Jibbon study area, Royal National Park, New South Wales, Australia. SE = standard error.

Variable	Slope	SE	z	P
<i>Fire ephemerals (PFT 4)</i>				
Intercept	−0.59	0.33	−1.81	0.07
Rainfall prior year	0.29	0.05	5.70	<0.01
Years since fire	−0.18	0.05	−3.30	<0.01
Rainfall prior year × years since fire	−0.33	0.07	−4.56	<0.01
<i>Rhizomatous resprouters (PFT 5)</i>				
Intercept	3.22	0.15	21.84	<0.01
Rainfall prior year	−0.11	0.008	−13.61	<0.01
Years since fire	−0.02	0.009	−2.69	<0.01
Rainfall prior year × years since fire	−0.22	0.01	−19.87	<0.01
<i>Perennial resprouting herbs (PFT 6)</i>				
Intercept	1.20	0.18	6.87	<0.01
Rainfall prior year	0.28	0.03	10.79	<0.01
Years since fire	−0.39	0.03	−13.90	<0.01
Rainfall prior year × years since fire	−0.10	0.04	−2.57	0.01

hints that important environmental drivers of habitat suitability were not captured in these variables. Importantly, duration of snow cover (i.e., number of days that snow is on the ground), rather than maximum snow cover depth per se, may be important, as this determines when mountain pygmy-possums first enter, and are then released from, winter hibernation, as well as the time during which bush rats can access and colonise snow-covered sites. The timing of snow thaw may also be crucial; earlier release from snow cover may create mis-matches in the activity of mountain pygmy-possums and one of their primary food sources, the migratory bogong moth that typically appears in the Austral spring (Common, 1954). Unfortunately, long-term data for these potentially important determinants of population dynamics of small mammal do not exist. The data hint, however, that suitable conditions for mountain pygmy-possum persistence are deteriorating, with

Table 4

Nanangroe Plantation Plot Network. Quasi-binomial generalized linear model results for bird species reporting rates and their responses to climate (mean annual rainfall and temperature) and survey year (1998–2015), Gundagai, New South Wales, Australia. SE = standard error.

Variable	Slope	SE	z	P
<i>Coracina novaehollandiae</i>				
Intercept	24.12	55.26	0.44	0.67
Rainfall	0.003	0.002	1.73	0.12
Temperature	0.83	0.43	1.93	0.09
Survey year	−0.02	0.03	−0.70	0.50
<i>Ocyphaps lophotes</i>				
Intercept	−225	66	−3.42	0.009
Rainfall	0.0001	0.001	0.09	0.93
Temperature	0.67	0.41	1.62	0.14
Survey year	0.16	0.03	3.23	0.01
<i>Philemon corniculatus</i>				
Intercept	72.66	67.35	1.08	0.31
Rainfall	−0.002	0.002	−0.96	0.37
Temperature	−0.19	0.50	−0.38	0.71
Survey year	−0.03	0.03	−1.02	0.34
<i>Pachycephala rufiventris</i>				
Intercept	−0.47	43.15	−1.08	0.31
Rainfall	0.00007	0.001	0.06	0.96
Temperature	0.76	0.32	2.38	0.04
Survey year	0.02	0.02	0.79	0.45
<i>Lichenostomus penicillatus</i>				
Intercept	147.3	31.7	4.64	0.002
Rainfall	−0.0005	0.0009	−0.59	0.57
Temperature	0.07	0.22	0.34	0.74
Survey year	−0.07	0.02	−4.64	0.002

bush rat numbers increasing either as a direct result of the changes in the environment (i.e., increasingly warmer summers, increasing frequency of poor snow cover), or indirectly via their effects on interspecific interactions, including competition.

Our analyses from the Nanangroe Plantation Plot Network revealed complex survey year and climate variable effects for several species of birds. Two species, the crested pigeon and the white-plumed honeyeater, exhibited an increase and a decrease in reporting rate over the duration of the study, respectively. The reasons for these changes remain unclear. In the case of the crested pigeon, the changes may be associated with the extensive human disturbance associated with timber harvesting and other kinds of management within the plantation as stands of radiata pine matured. The decline in reporting rate for the white-plumed honeyeater is likely associated with competition with another species of native honeyeater, the yellow-faced honeyeater, which has become abundant in plantation-dominated areas over the past two decades (see [Lindenmayer et al., 2015](#)).

Significant relationships existed between the reporting rates of each of three bird species and climate variables. The increased reporting rates of the black-faced cuckoo-shrike and rufous whistler were associated positively with increased temperature. The black-faced cuckoo-shrike and noisy friarbird responded to rainfall, but positively and negatively, respectively. Again, the reasons for these patterns remain unclear. However, weather variables such as rainfall or temperature affect bird populations in ecosystems worldwide ([Tayleur et al., 2015](#); [Gardner et al., 2016](#)). Weather can affect birds positively by generating pulses of key resources such as food ([McGoldrick and Mac Nally, 1998](#); [Barea and Watson, 2007](#)), but may influence species in other ways also, such as when temperature extremes disrupt nesting behavior ([Hennan et al., 2015](#); [Mariette and Buchanan, 2016](#)). The increase in mean and frequency of extreme temperature events in the study region may favor some species of birds, such as the black-faced cuckoo-shrike and rufous whistler, over others leading to long-term shifts in species composition.

4.2. Indirect effects of climate change on biota through a change in fire regimes

Fire-vulnerable sandstone tropical heathlands in northern Australia are listed as part of a nationally endangered community, with over half of the constituent shrub species functioning as obligate seeders ([Commonwealth of Australia, 2012](#)). The impacts of frequent fires on the population sizes and persistence of obligate seeder shrubs are generally well understood, as is the magnitude of the associated regional conservation management challenge ([Russell-Smith et al., 2012](#); [Keith et al., 2014](#)). Similarly, small mammal communities may respond negatively to increased fire frequency ([Andersen et al., 2005](#); [Radford et al., 2015](#)), as well as to increased fire intensity ([Andersen et al., 2005](#)), and extent ([Lawes et al., 2015](#)). Population declines are due primarily to reduced structural complexity and composition of vegetation with frequent fire ([Bowman, 1998](#)), causing the loss of a wide array of shelter and food resources, as well as increasing exposure to predation by feral cats ([McGregor et al., 2015](#)). Vertebrate monitoring across the Three Parks Savanna Fire-Effects Plot Network has provided some of the most compelling evidence of small mammal declines in northern Australia (e.g., Kakadu plots, [Woinarski et al. \(2010\)](#)). More broadly, about half of the tropical savanna's 40 small to medium-sized mammals have undergone substantial declines in range and density ([Fitzsimons et al., 2010](#); [Woinarski et al., 2011](#)). Intensive fire management that is required for maintenance or recovery of small mammals is aimed at increasing the extent of longer-unburnt habitat and in delivering fine-scale patch burning at hectare scales ([Ziembicki et al., 2015](#)). However, fire management is likely to become increasingly challenging, with predicted significantly increasing temperature conditions (up to 5 °C, and a 2–20-fold increase in the number of days with extreme temperatures (>35 °C) depending on different emissions scenarios ([CSIRO and Bureau of Meteorology, 2015](#))), likely to promote the intensity and

frequency of regional fires. Indeed, all extreme temperature events at the Three Parks Savanna Fire-Effects Plot Network occurred during post-2005 surveys. Developing effective fire management responses for biodiversity conservation outcomes across Australia's northern savannas is a critical challenge ([Russell-Smith et al., 2017](#)).

4.3. Climate change may alter climate-mediated fire responses

The responses of temperate heathland vegetation represented by the Upland Heath Swamps Plot Network depend on interactions between species' life history (represented by functional types), time since fire and the dynamics of post-fire rainfall. One plant functional type (PFT4) includes species that depend entirely on seedling recruitment for population persistence. These taxa have relatively short-lived standing plant phases and long-lived seedbanks. Their seeds are stimulated to germinate by fire and reach maximum abundance in stems within a year and decline relatively rapidly thereafter (and hence show a negative relationship with time since fire). Recruitment success depends on rainfall amount. PFT6 plants show a similar response, but the mechanism is different because these species resprout after fire via non-proliferating underground organs and are unlikely to maintain long-lived seedbanks. Standing PFT6 plants may persist longer after fire, but are sensitive to competition from developing overstorey shrubs, and hence have a negative relationship with time since fire. PFT5 species have underground organs that support post-fire resprouting, but also promote clonal proliferation. Seedling recruitment appears relatively rare compared to other PFTs. This group is more resilient to time since fire than other PFTs, and has a different relationship with rainfall. The increase in mean temperature and frequency of extreme temperature events may increase the length of the wildfire season, shorten fire return intervals, and increase fire intensity ([Flannigan et al., 2009](#); [Liu et al., 2010](#); [Jolly et al., 2015](#)). PFTs can be used to predict shifts in species composition due to changes in fire regimes ([Keith and Tozer, 2012](#)); however, rainfall may be important to accurately predict changes in species composition.

4.4. Implications for conservation

Our long-term ecological research provides many useful insights for conservation organisations, land managers and governments responsible for managing biodiversity. By identifying key environmental drivers and species that are influenced by them, we can predict how populations respond if these drivers change over time. We found no evidence of non-linear threshold behavior in the systems examined; even in the desert ecosystem that exhibited irruptive responses to major rainfall events, the responses were broadly repeatable, if not differing in detail, between events. For now, this means that long-term research has provided managers with a degree of confidence in predicting responses to environmental change within these ecosystems. Long-term research is also critical to interpreting surprise responses if ongoing environmental change pushes ecosystems toward unforeseen tipping points.

Monitoring of multiple populations allows identification of community-level changes in which the effects of climate are mediated through changes in biotic interactions ([Walther et al., 2002](#); [Alexander et al., 2015](#)). For example, the different trends in small mammal captures may be driven directly by climate, or indirectly via climatic effects on interspecific interactions ([Alexander et al., 2015](#)). Similarly, climate may be important as a mediator of fire effects for some functional groups of plants in temperate heathlands.

Because of a rapidly changing climate, managers need to identify declines in populations relative to the natural temporal variation ([Magurran et al., 2010](#)). Our long-term analysis allowed such trends to be identified, even in highly stochastic environments, such as deserts. Declines were identified in some species of birds and small mammals from forest and alpine environments, while other species increased over time. Information gained from long-term studies can be used by

managers to assess species most at risk of local extinction and ecosystems most at risk of collapse.

Responses of biodiversity to environmental change are context-specific. The outcomes we observed were varied and attributable to qualitatively different mechanisms of response to environmental change. This demands not only methods of risk analysis that accommodate ecosystem-specific measures of functional change (Keith et al., 2013), but an expansive network of monitoring across contrasting ecosystems with designs that are tailored to the key biota and drivers of those systems. Approaches that apply standardised methods across systems may thus be ill-equipped to detect change and diagnose its causes. The magnitude and frequency of mean and extreme climate events are changing in many biomes, suggesting that long-term monitoring of biodiversity will become increasingly important for detecting resultant changes in species populations. Long-term monitoring plots facilitate the detection of non-linear relationships between species and climate, including the identification of environmental thresholds in places where resource-pulses are infrequent or unpredictable (Van Etten, 2009; Morton et al., 2011). However, responses to change in one context or site cannot be extended to other ecosystems or geographical areas without caution (Magurran et al., 2010; Peters et al., 2012). In Australia, a coordinated (national) long-term monitoring framework (i.e., LTERN) allowed us to find contrasting species responses to climate and disturbance across diverse biomes. We conclude that there is a need to establish and fund long-term monitoring programs across a representative suite of Australian ecosystems, consistent with international objectives for long-term ecological research (Hobbie et al., 2003; Robertson et al., 2012). Where feasible, any new investment should strategically build on pre-existing long-term research.

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